12

Annelida

Richard A. Robison

Various benthic, soft-bodied animals independently developed locomotion without limbs. The mechanical requirements for this type of locomotion have commonly produced a convergence in external form resulting in a bilaterally symmetrical, elongate body. Most animals of this form have been called worms, and, at one time, all worms were assigned to a single phylum, Vermes. Subsequent investigations have demonstrated several distinct grades of worms, causing repeated revisions in classification. Currently, as many as 14 worm phyla are recognized, which is about one-half of all the animal phyla (see Chapter 2, Table 2.1).

Considering the usual requirements for preservation of fossils, it should not be surprising that, except for hardened jaw apparatuses in a few groups, remains of fossil worms have seldom been discovered. Various kinds of worm burrows, tracks, castings, and tubes are much more commonly encountered; however, they rarely provide information useful for taxonomic identification of their makers. Because only one phylum, the Annelida, has an appreciable fossil record, it is the only worm phylum treated in this book.

The most familiar annelids are the earthworms (Figure 12.1, *D*), which are common in garden soil. Less familiar groups are the leeches and marine bristleworms (Figure 12.1, *A* to *C*). In addition to their elongate, bilaterally symmetrical bodies, annelids are at the triploblastic coelomate grade and are characterized by a metamerous coelom (see Chapter 2), which is divided into numerous segments, each with a repetition of body parts. A high degree of segmentation—the basis for the phylum name (from the Latin, *annelus*, meaning little ring)—is a characteristic that distinguishes the Annelida from all other phyla except the Arthropoda, which differs by the presence of an external skeleton, jointed appendages, and great reduction of the coelom. A secondary loss of segmentation is rare in specialized sessile annelids, but internal vestiges can still be recognized.

Annelids had almost certainly evolved by Proterozoic time. Although body fossils are rare, an increasing abundance and variety of tubes and trace fossils in Phanerozoic strata attest to a history of expanding annelid diversity during the last 600 million years. Today, annelids occupy many habitats extending from the deep oceans to high mountains and from equatorial to polar regions.

Fossils of these inconspicuous, soft-bodied creatures have had little use in biostratigraphy. However, because of the capacity of some annelids to ingest and modify great volumes of soil and sediment, their influence on the geologic record may surpass that of any other animal phylum. For example, densities of up to 5000 annelids per square meter are not unusual in marine sediments. On some sandy intertidal beaches, densities of 32,000 burrowing annelids per square meter have been reported. Repeated ingestion by these worms totals as much as 3 metric tons of sand per square meter per year. On land, densities of 50 to 500 earthworms per square meter are common, depending on soil type. These might move as much as 5 kg of castings per square meter to the surface each year. The castings are some of the world's finest fertilizer, being rich in nitrates, phosphates, and potash.

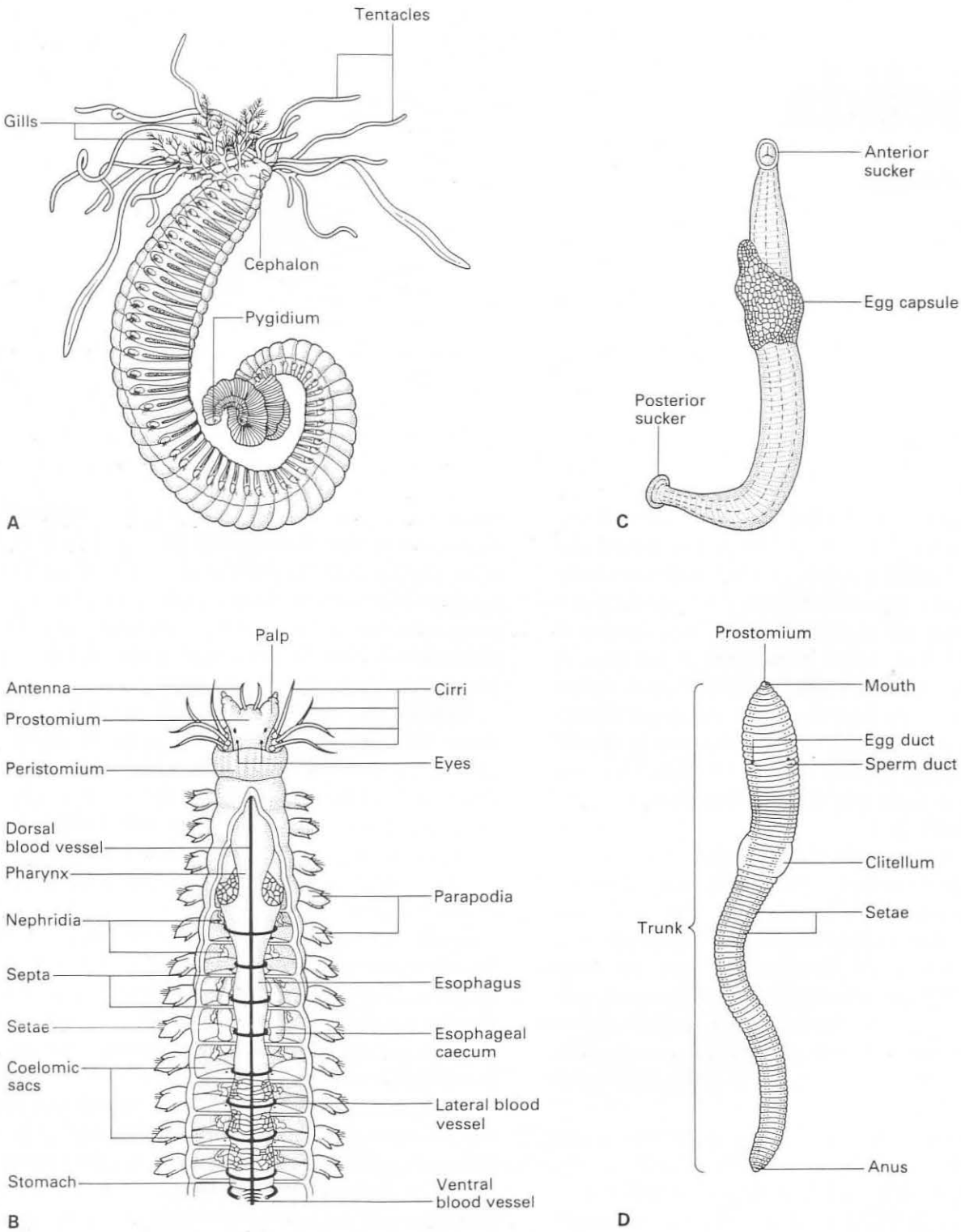

Figure 12.1. Morphology of representative modern annelids. **A**, *Amphitrite*, a tube-dwelling marine polychaete. **B**, General arrangement of internal organs in the anterior part of *Neanthes*, a crawling and swimming marine polychaete. **C**, *Hirudinaria*, a freshwater leech with an egg capsule being formed while the body is held in place by suckers. **D**, Ventral view of *Lumbricus*, the common earthworm. (**A**, **B**, and **D** modified from Brown, F. A. *Selected invertebrate types*. Copyright © 1950 by John Wiley & Sons, Inc. Reprinted by permission. **C** modified from Fretter, V.; Graham, A. *A functional anatomy of invertebrates*. New York: Academic Press, Inc.; 1976.)

Morphology

Adaptations of the annelids to many habitats and niches have resulted in a highly diverse phylum. The length of mature individuals ranges from less than 1 mm in some marine annelids that dwell between sand grains to almost 400 cm in some giant Australian earthworms. Representative annelid morphology is illustrated in Figure 12.1.

External features

The body is bilaterally symmetrical and is divided into a short head region or **cephalon** with a mouth and concentration of sensory apparatus, a long segmented **trunk**, and a tiny postsegmental **pygidium** (Figure 12.1). This body division is generally most apparent in sessile forms and least conspicuous in vagile forms (forms free to move about). The exterior covering is a thin nonchitinous cuticle that is secreted by the epidermis. Muscularly movable, bristlelike **setae** are commonly implanted in the soft body wall and aid in anchoring some annelids in either their burrows or tubes, assist in surface locomotion, or even aid in swimming. The number and distribution of setae are useful definitive characters at higher taxonomic levels; and setal form, which is highly variable, is useful at lower taxonomic levels. Many annelids also have highly developed glands for secreting slime, building tubes, burrowing, or ingesting food.

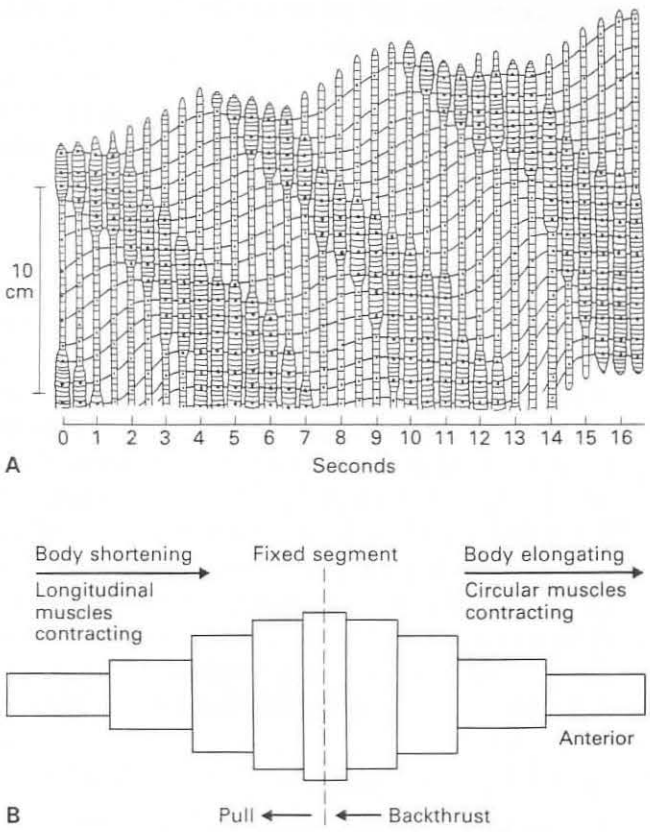

Figure 12.2. Annelid locomotion. **A**, Diagram prepared from motion pictures showing successive stages in the locomotion of an earthworm. Regions of the body with contracted longi tudinal muscles are drawn twice as wide as those with contracted circular muscles and are also marked by larger dots. Progression begins as circular muscles contract in the anterior segments and continues as successive waves of circular and longitudinal contractions pass backward along the body. The track of individual points on the worm's body and their movements relative to each other are shown by the lines running obliquely forward from left to right on the diagram. **B**, Forces acting upon the stationary segment and adjacent moving segments of an earthworm performing peristalsis. (A from Gray, J.; Lissmann, H. W. *Journal of Experimental Biology* 1938 v. 15, p. 506–517. B modified from Clark, R. B. *Dynamics in metazoan evolution*. Oxford: Oxford University Press; 1964 p. 120.)

Degree of cephalization, or fusion of anterior segments, varies according to adaptation. In many marine annelids the cephalon is divided into two parts. A presegmental prostomium in front of the mouth may carry unjointed sensory **antennae** and stout feeding **palps** (Figure 12.1). A mouth-bearing peristomium may be fused with one or more posterior segments and carry long slender feeding and sensory **tentacles** and shorter sensory **cirri**. Eyes, if present, may be simple or complex and small to large.

The trunk contains few to many segments, all tending to be similar in vagile annelids but differentiated to form anterior thoracic and posterior abdominal regions in some sessile marine groups. **Parapodia** are unjointed fleshy locomotory appendages on the lateral body walls of many marine annelids. Typically the parapodia carry terminal bundles of setae and are internally supported by slender chitinous rods (aciculae) that are moored by basal muscles.

The pygidium is a small postsegmental unit with the anus on its ventral surface.

Internal features

The basic annelid body plan is well illustrated by the common earthworm. In simplest form, it consists of a flexible body wall containing antagonistic layers of outer circular muscles and inner longitudinal muscles enclosing a fluid-filled coelom. Mechanically, the confined coelomic fluid provides a central support for the body and functions as a **hydrostatic skeleton.** Multiple transverse septa partition the coelom and limit the transmission of fluid pressure, thereby enabling localized changes in shape. Locomotion is accomplished by peristalsis, an action generated by successive waves of muscle contractions that pass backward along the body (Figure 12.2, *A*). In any part of the body, simultaneous contraction of

circular muscles and relaxation of longitudinal muscles results in elongation, whereas reverse muscle activity results in shortening (Figure 12.2, *B*). Those parts of the body are fattest where longitudinal muscles are maximally contracted, and by wedging those fat parts against the wall of a burrow, thrust can be exerted. Simultaneous extension of setae provides additional resistance to slipping. Each segment in succession becomes stationary as a muscle wave passes backward.

This simple annelid body plan has advantages and limitations. It represents a significant functional advance over the unsegmented coelomate worms (such as sipunculids and echiuroids), in which individual muscle contractions influence the entire hydrostatic skeleton. In those animals, localized change in shape is difficult, and rapid movement is excessively wasteful of energy. Thus their mode of life is necessarily rather sessile. On the other hand, advanced lever systems are impossible for soft-bodied animals, and annelid locomotion over a flat substratum is much less efficient than that of arthropods and higher chordates.

Most other internal features also show a clear segmental arrangement of parts (Figure 12.1, *B*) and include the following:

1 A central nervous system consisting of paired cerebral ganglia merging posteriorly into a ventral cord with lateral nerve branches to each segment.

2 A closed circulatory system with median dorsal and ventral blood vessels joined in each segment by vessels to the gut and body wall and one to several pulsating heart-like organs.

3 An alimentary tract with pharynx, esophagus, stomach, and intestine.

4 An excretory system with simple to complex pairs of **nephridia** in most segments.

Like tubules in the human kidney, these nephridia extract wastes from the blood and coelomic fluid. Respiration is accomplished by gaseous exchange through the body wall or by gills in some tube dwellers.

Great variation has been superimposed on the basic, and presumably primitive, annelid body plan. In many marine annelids, parapodia project from the lateral body walls and are operated by a complex series of muscles. Secondary adaptation to a sessile life by some marine worms has been accompanied by a corresponding reduction in septa to become no more than suspensory muscles for the gut, and they no longer function as coelomic seals between segments. In the parasitic leeches, septa have disappeared, and the coelom is much reduced or almost absent, being largely replaced by connective tissue.

Reproduction

Reproduction in annelids may be sexual, asexual, or both. The sexes are separate in most marine annelids, but the reproductive system varies from simple to extremely complex. Gametes may be released directly into the sea or fertilized eggs may be deposited in gelatinous balls and strands. Among some tube dwellers, the eggs may be brooded within the tube. Earthworms and leeches are **hermaphroditic** (sexes united) and possess complex glands associated with reproduction. The **clitellum** (Figure 12.1, *D*) of earthworms and leeches is a swollen glandular region that secretes a mucous ring or capsule into which eggs and sperm are discharged. In what is thought to be a primitive means of reproduction, the fertilized eggs of some marine annelids develop into ciliated spheroidal larvae called **trochophores**. Other annelids reproduce asexually by budding or related processes.

Classification

Three major annelid classes, Polychaeta (bristleworms), Oligochaeta (earthworms), and Hirudinea (leeches), are generally recognized, but disagreement continues over the status of additional classes that have been proposed. Some of the more useful taxonomic characters of living annelids are: structure of the reproductive system; number, distribution, and form of setae; presence or absence of parapodia; structure and appendages of the cephalon; and structure and distribution of nephridia. Some of these characters are rarely, if ever, preserved in fossils. Hence, confident taxonomic assignment of some fossils to family, order, and even class may not be possible.

CLASS POLYCHAETA (Figure 12.1, *A* and *B*)

Morphology highly variable and strongly dependent on mode of life. Sexes usually separate with gonads in numerous segments; egg and sperm ducts simple. Parapodia common and bearing numerous setae in distinct bundles. Cephalic appendages common in sessile forms. (Possibly Proterozoic, Cambrian to Holocene; about 150 genera.)

Polychaetes usually occupy marine, rarely freshwater, and more rarely terrestrial habitats. Many are deposit and filter feeders, others are predators or scavengers, and a few are parasites.

During the first half of this century, the polychaetes were usually divided into two orders or subclasses of

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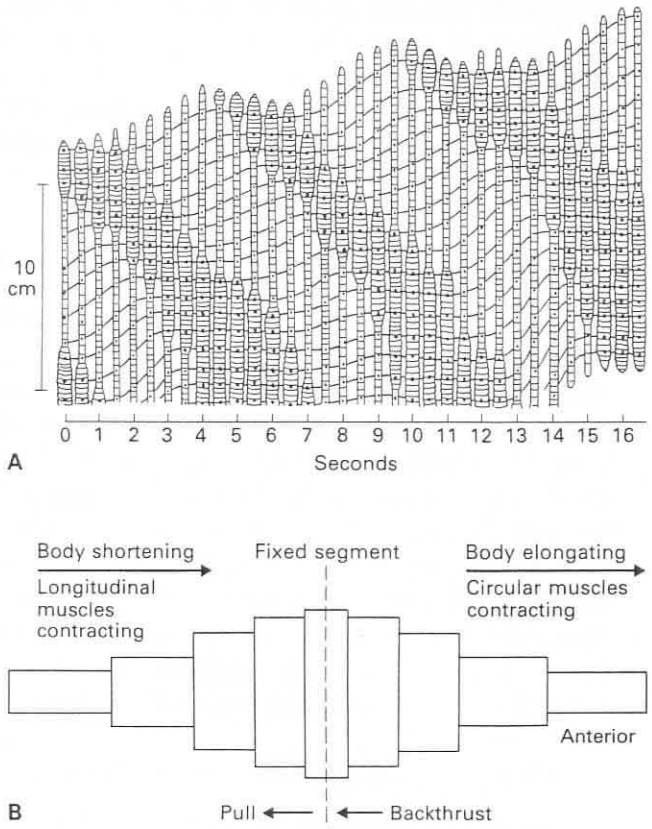

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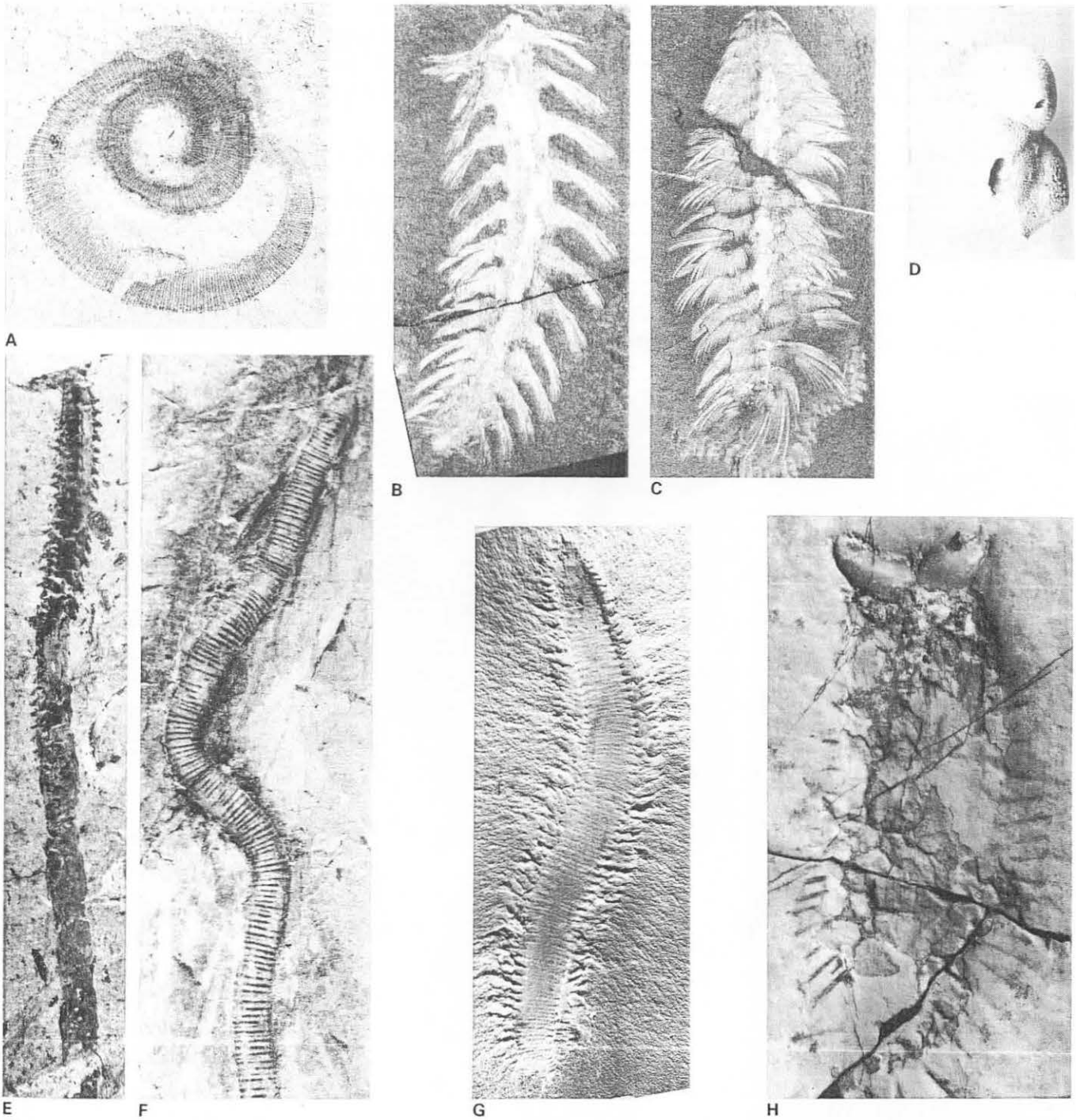


Figure 12.4. Examples of annelid body fossils and parasitic cysts. **A**, *Palaeoscolex* (Middle Cambrian, Utah), about 125 mm long if fully extended; coiling of this type in modern polychaetes is often induced by anaerobic conditions. **B** and **C**, *Burgessochaeta*, a possible burrower, and *Canadia*, a possible benthic swimmer; each with prominent but differently arranged setae, and each about 30 mm long (from Burgess Shale of Middle Cambrian age, British Columbia). **D**, Two perforated cysts formed on the arm of a Pennsylvanian crinoid in response to infestation of parasitic myzostomarian annelids. **E**, A polychaete, *Trentonia*, preserved at the end of its trace (Middle Ordovician, Quebec), illustrated portion about 60 mm long. **F**, Anterior part of *Protoscolex*, class undetermined (Upper Ordovician, Kentucky). **G**, A Late Mississippian polychaete, *Astreptoscolex* (Bear Gulch, Montana), about 100 mm long. **H**, Anterior part of *Eunicites* with jaw apparatus in place (top) and acicula preserved along trunk segments (Solenhofen Limestone of Middle Jurassic age, Germany); illustrated part about 40 mm long. (**A** from Robison, R. A. *Journal of Paleontology* 1969 v. 43, p. 1169–1173. **B** and **C** from Conway Morris, S. *Philosophical Transactions of the Royal Society of London* 1979 v. 285, p. 277–284. **D** from Welch, J. R. *Journal of Paleontology* 1976 v. 50, p. 218–225. **E** from Pickerill, R. K.; Forbes, W. H. *Canadian Journal of Earth Sciences* 1978 v. 15, p. 659–664. **G**, courtesy F. R. Schram; **H**, courtesy A. Seilacher.)

nearly equal size, Errantia and Sedentaria—the names reflecting their modes of life. More recently, depending on the author, that bipartite classification has been rejected in favor of 8 to 17 orders that include about 60 to 80 families.

Members of a few orders, and in particular the Eunicida, possess pharyngeal jaws composed of several hardened organic elements that paleontologists call **scolecodonts** (Figure 12.3). In the living animal these are joined by muscle tissue and cuticle but are usually found separated as fossils. The jaw apparatus typically includes a ventral pair of **mandibles** for chewing, a series of asymmetrically or incompletely paired **maxillae** for manipulating food, and a basal pair of **carriers** that support the posterior maxillae. Scolecodonts superficially resemble conodonts (see Chapter 20) but differ in composition and microstructure.

CLASS OLIGOCHAETA (Figure 12.1, *D*)

Hermaphroditic earthworms with gonads limited to a few anterior segments. Complex glands are associated wth specialized sperm and egg ducts; clitellum present at maturity. Cephalon indistinct and parapodia absent. Setae segmentally arranged, only rarely in bundles, and may be absent.

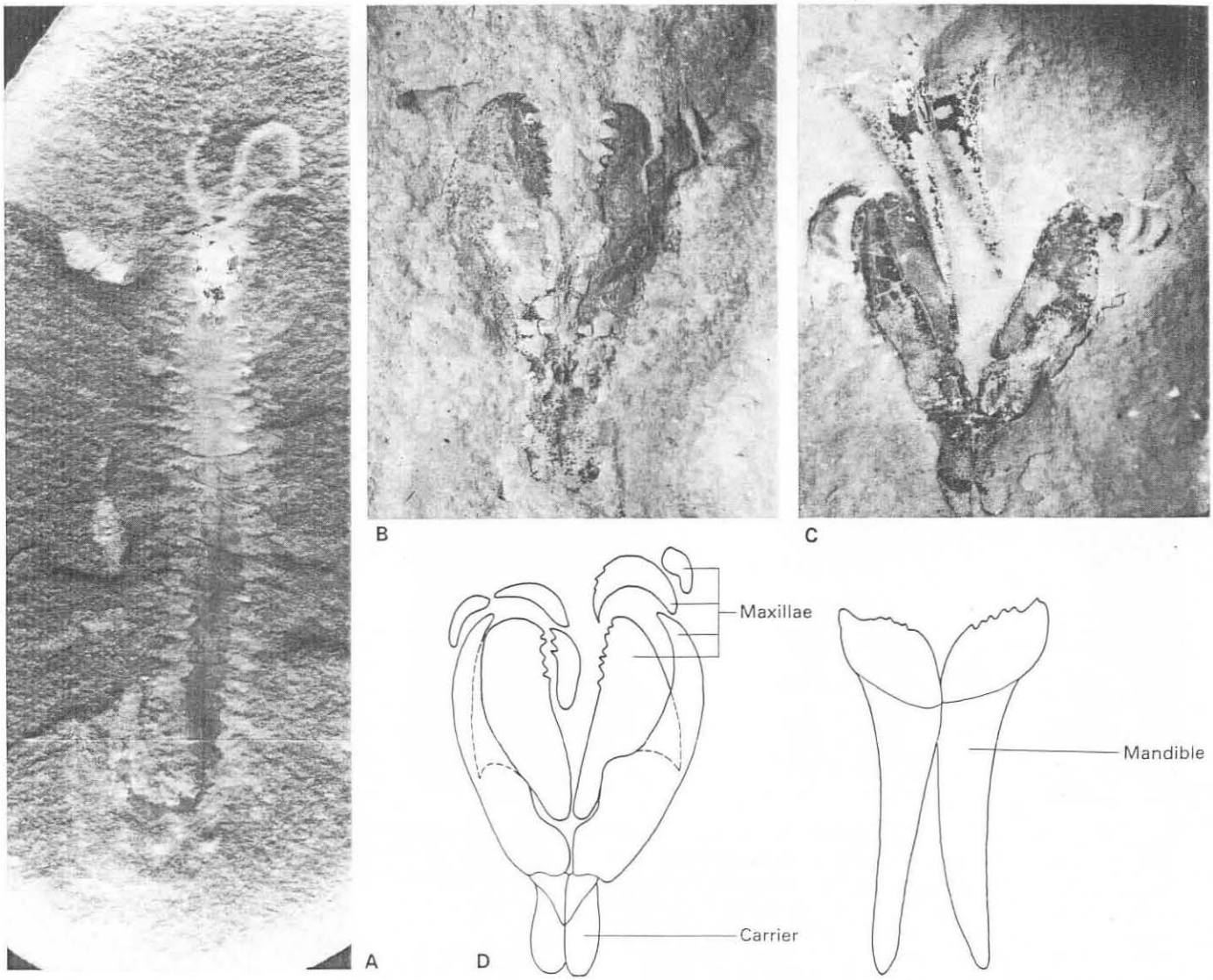
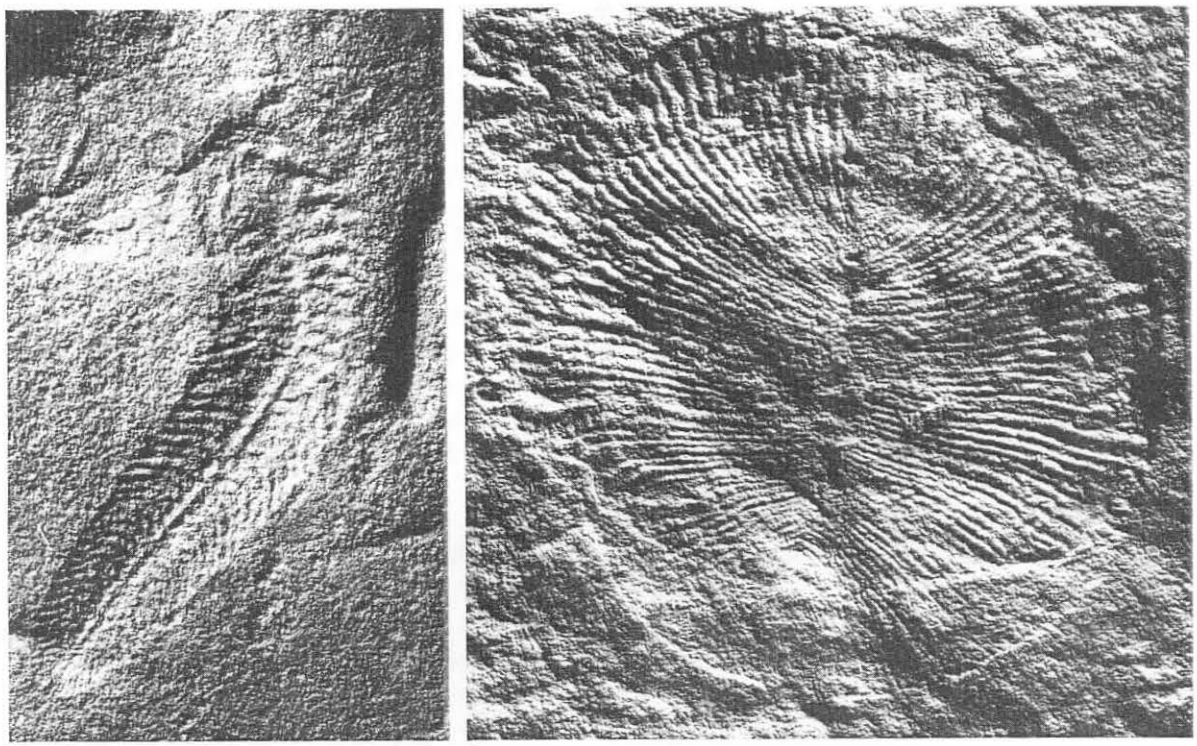


Figure 12.3. Jaw apparatus in the polychaete *Esconites* (order Eunicida) of middle Pennsylvanian age from Illinois. A, Complete specimen, about 60 mm long, with antennae, gills, and a poorly preserved jaw apparatus in place. B, Enlarged ventral view of associated jaw elements (scolecodonts) from another specimen with maxillae above and carriers below; entire apparatus about 6 mm long. C, Ventral view of another jaw apparatus with mandibles above and spread maxillae below. D, Dorsal reconstruction of jaw apparatus based on many specimens. (Modified from Thompson, I.; Johnson, R. G. *Fieldiana: Geology*; 1977.)



A B

Figure 12.5. Examples of Proterozoic fossils from Australia that have been assigned to the Annelida by some specialists. A, *Spriggina*, an elongate genus that ranges up to 4 cm in length and resembles modern pelagic polychaete annelids of the family Tomopteridae; however, the absence of well-developed parapodia and the enlarged head region, among other features, also suggest an arthropod affinity. B, *Dickinsonia*, a flat ovoid genus, ranging up to 60 cm in length, resembles an unusual modern polychaete that is parasitic on sponges; possible affinities with the flatworms (phylum Platyhelminthes) is an alternative preferred by some workers. (Courtesy M. F. Glaessner.)

chaetes was the development of hardened jaw elements or scolecodonts. These elements are known to range from the Ordovician to the Holocene, and they are most abundant in shallow marine deposits. Although they hold potential for biostratigraphic zonation, scolecodonts have received relatively little study, largely because of taxonomic difficulties. The elements, which are parts of an assemblage or jaw apparatus, are usually found dissociated. Moreover, some element types are homeomorphic, being found in more than one kind of natural assemblage. In a few instances natural assemblages of scolecodonts have been found associated with other body remains (Figure 12.3), and sometimes by careful study the jaw apparatuses can be reconstructed from dissociated material (Figure 12.6); however, much more work will be necessary before the biostratigraphic potential of these fossils is fulfilled.

Trace fossils of probable annelid origin are abundant in many Phanerozoic marine deposits. A large number of the burrows and trails were probably made by polychaetes, but other animals also leave similar traces, and identification of the trace maker is seldom possible (see Chapter 21 for examples and further discussion).

For protection, some polychaetes secrete sturdy calcareous tubes in which to live, others construct leathery tubes of mucus, and still others build agglutinated tubes by cementing sand grains, shell fragments, or miscellaneous debris with mucus. One common calcareous form, *Spirorbis* (Figure 12.7, *A* and *B*), produces small, solitary, coiled tubes that are typically found attached to shells of other fossils. It has a geologic range from Ordovician to Holocene. Another long-ranging (Silurian to Holocene) and cosmopolitan genus is *Serpula* (Figure 12.7, *C*), which usually lives in groups and produces long, slender, coiled or contorted tubes. From the Jurassic onward, abundant serpulid tubes locally form the framework of extensive organic layers and mounds. Other polychaetes build closely packed tubes, both calcareous (Figure 12.7, *D*) and agglutinated (Figure 12.7, *E*), which may form wave-resistant reefs along tropical and subtropical coasts. One such modern example is essentially continuous along more than 300 km of the southeastern coast of Florida.

Although their numbers are great in modern soils, fossilized Oligochaeta have not been definitely identified. One genus (Figure 12.4, *F*) from Ordovician and Silurian

Most oligochaetes dwell in moist burrows in the soil and feed on decaying vegetable matter. Some live in fresh water, and a small number are marine. A few fossils have been assigned to the Oligochaeta, the oldest being Ordovician in age. However, the identifications of all such specimens are open to serious question because of inadequate preservation of critical taxonomic features.

CLASS HIRUDINEA (Figure 12.1, *C*)

Hermaphroditic and parasitic leeches with anterior and posterior suckers for attachment and aid in locomotion. Parapodia and septa absent, coelom much reduced, and setae usually absent.

Most hirudineans inhabit fresh water, but some are marine, and a few live in damp places on land. Their unusual morphology clearly reflects a secondary adaptation to their parasitic mode of life. Except for two genera of questionable identity from the Jurassic of Germany, hirudineans are unknown as fossils.

Other annelids

A small group of highly specialized, parasitic marine worms, the Myzostomaria, has an unusual discoid body with incomplete septa and five pairs of parapodia, each with a small chitinous hook on the end. Members resemble polychaetes in producing trochophore larvae but resemble oligochaetes and hirudineans in being hermaphroditic. Taxonomic assignment has been controversial, ranging from family or order under the Polychaeta to inclusion in a separate phylum, but recognition as an annelid class seems to be a developing consensus.

Myzostomarians infest echinoderms, particularly crinoids. Generally, groups of two or more myzostomarians invade tissue between skeletal plates of the crinoid arms, pinnules, and cups. The host secretes calcium carbonate to partially seal off the parasites and thereby produces a perforated gall or cyst (Figure 12.4, *D*). Such structures range in age from at least Pennsylvanian to Holocene. Superficially similar swellings are present on crinoid stems as old as Ordovician; however, these probably represent a different type of parasite of uncertain affinities.

Origin and evolution

The meager fossil record provides little knowledge regarding the origin of annelids and only a sparse and very fragmentary outline of their evolutionary history. Additional information from comparative anatomy and embryology can be instructive.

Initial segmentation of the annelid coelom probably enabled peristaltic burrowing. Support for this conclusion is found in the fact that when its circular muscles contract, a simple annelid body must become circular in transverse section, thus making peristaltic locomotion ideal in burrows. In comparison, peristaltic locomotion is poorly suited to movement on flat surfaces where the amount of body-to-surface contact is minimal. The advance in locomotion over that possible in unsegmented coelomates was not achieved without cost, however, because compartmentation of the coelom requires repetition of most organ systems and makes specialization and concentration of function in those systems difficult, if not impossible.

When annelids first appeared is uncertain. A few genera of Proterozoic body fossils (Figure 12.5) have been assigned to the Annelida. None of these is of typical annelid form, however, and alternative phyletic assignments are preferred by some specialists. The attribution of a number of Proterozoic trace fossils to an annelid origin is also open to question. Nevertheless, the variety of burrows leaves little doubt that annelids were in existence at least by Proterozoic time. It is generally concluded that the ancestral annelid was a vagile marine burrower, had separate sexes that spawned into the sea, and lacked parapodia and anterior appendages. It may have resembled *Palaeoscolex* (Figure 12.4, *A*), which is first known from the Lower Cambrian.

Although fossils are rare, available specimens show enough diversity to indicate extensive adaptive radiation among early Paleozoic polychaetes. The famous Burgess Shale of Middle Cambrian age has yielded six genera (Figure 12.4, *B* and *C*) from one locality in western Canada. Several other genera from the Burgess Shale that were formerly assigned to the Annelida have recently been reassigned to other phyla.

Polychaete parapodia represent a further advance in locomotion. It has been suggested that they were developed as aids to crawling in a medium too fluid for effective peristaltic burrowing. A likely environment for such evolution is the nutrient-rich flocculent layer immediately above many shallow sea floors. Because parapodia provide little assistance in swimming, it seems improbable that they evolved as an adaptation to aid that type of locomotion. Parapodia are first definitely known from the Middle Cambrian (Figure 12.4, *B* and *C*), and they are present on many later fossil polychaetes (Figure 12.4, *E*, *G* and *H*).

Another important event in the evolution of poly-

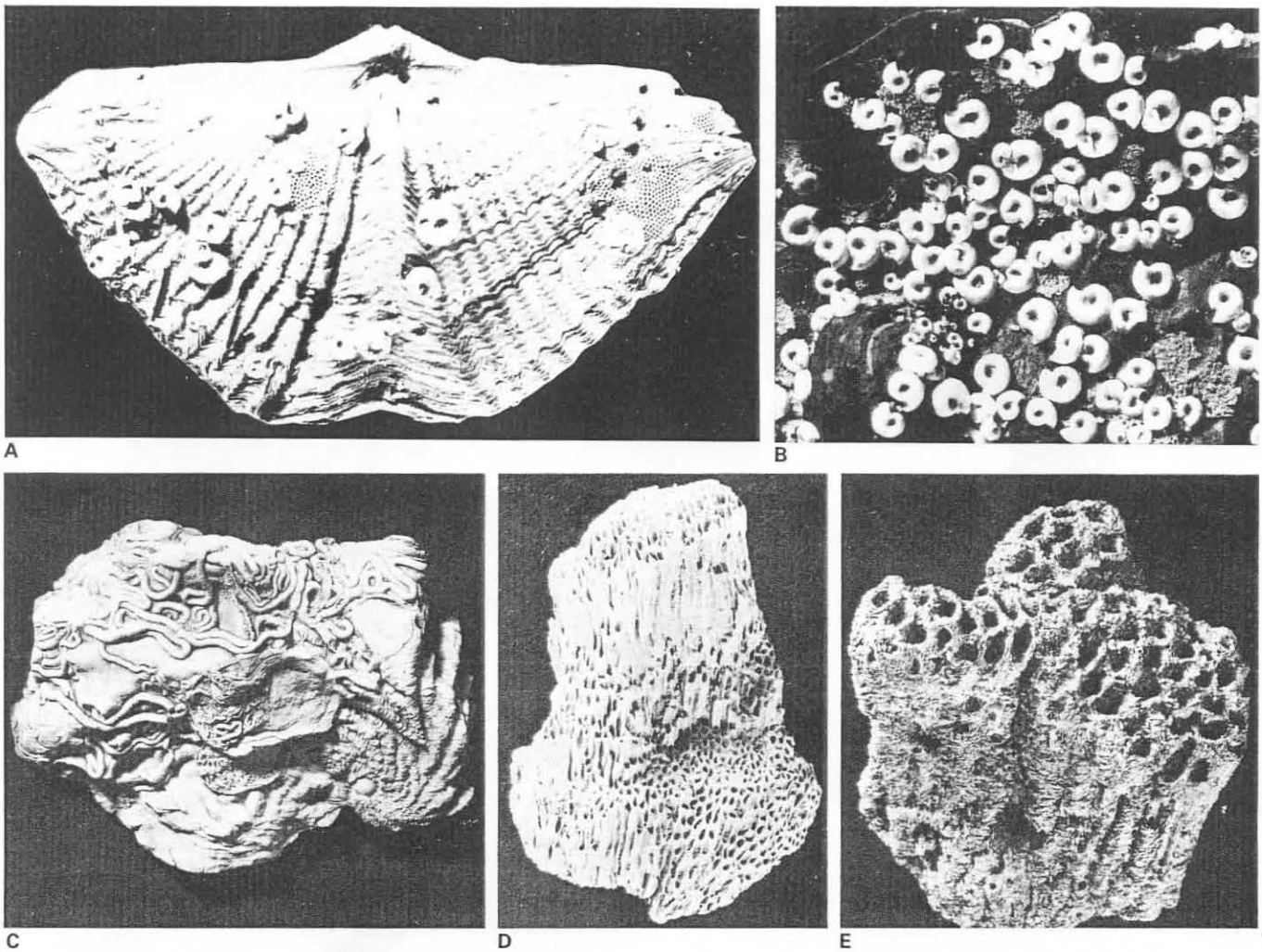


Figure 12.7. Polychaete tubes. **A**, *Spirorbis* and bryozoans encrusting a Devonian brachiopod from Ontario. **B**, *Spirorbis* and bryozoans encrusting modern seaweed from Newfoundland. **C**, *Serpula* encrusting a Cretaceous oyster from Texas. **D**, *Dodecaceria*, modern calcareous tubes from California. **E**, *Phragmatopoma*, modern agglutinated tubes from Florida. (Photos by M. Frederick.)

features obviously correlate with the adaptation from marine to terrestrial habitats.

A close relationship between the oligochaetes and hirudineans is indicated by shared possession of several derived features, especially those of the reproductive and excretory systems. However, the abandonment of a burrowing habit for one of parasitism resulted in additional fundamental changes in the hirudineans. Peristaltic locomotion aided by setae was exchanged for crawling with a looping motion aided by suckers, and some are capable of swimming. These activities greatly reduce the need for a segmented hydrostatic skeleton. Consequently, the hirudinean coelom has been reduced, and the septa have been lost.

Supplementary reading

Clark, R. B. *Dynamics in metazoan evolution*. Oxford: Clarendon Press; 1964. Excellent functional analysis of the origin of the coelom and segments.

Clark, R. B. Systematics and phylogeny: Annelida, Echiura, Sipuncula. In: Florkin, M.; Scheer, B. T., editors. *Chemical zoology*, vol. 4. New York: Academic Press, Inc.; 1969. Good review of the classification and evolution of annelids and some related groups.

Conway Morris, S. Middle Cambrian polychaetes from the Burgess Shale of British Columbia. *Philosophical Transactions of the Royal Society of London* (B. Biological Sciences) 285: 227–274; 1979. Redescription and analysis of some extraordinarily well-preserved, early annelids.

Edwards, C. A.; Lofty, J. R. *Biology of earthworms*, 2nd ed. London: Chapman & Hall; 1977. General account of oligochaetes with a key to common genera.

marine deposits has previously been referred to this class; however, representatives show no evidence of a clitellum. Moreover each segment has two rings of small nipplelike structures that may have held setae, and no modern oligochaetes are known to possess double rings of setae. Affinities of this genus remain in doubt. One other possible representative of the class is an annulated burrow cast from terrestrial Paleocene deposits in Wyoming.

The oligochaetes exhibit a combination of primitive and derived characters. On one hand, they have mostly remained vagile burrowers with primitive segmentation and no appendages. On the other hand, oligochaete nephridia have become highly specialized for reducing the loss of body fluids. Hermaphroditism is a specialization advantageous where mates or water for transport of gametes are not easily available. The latter two

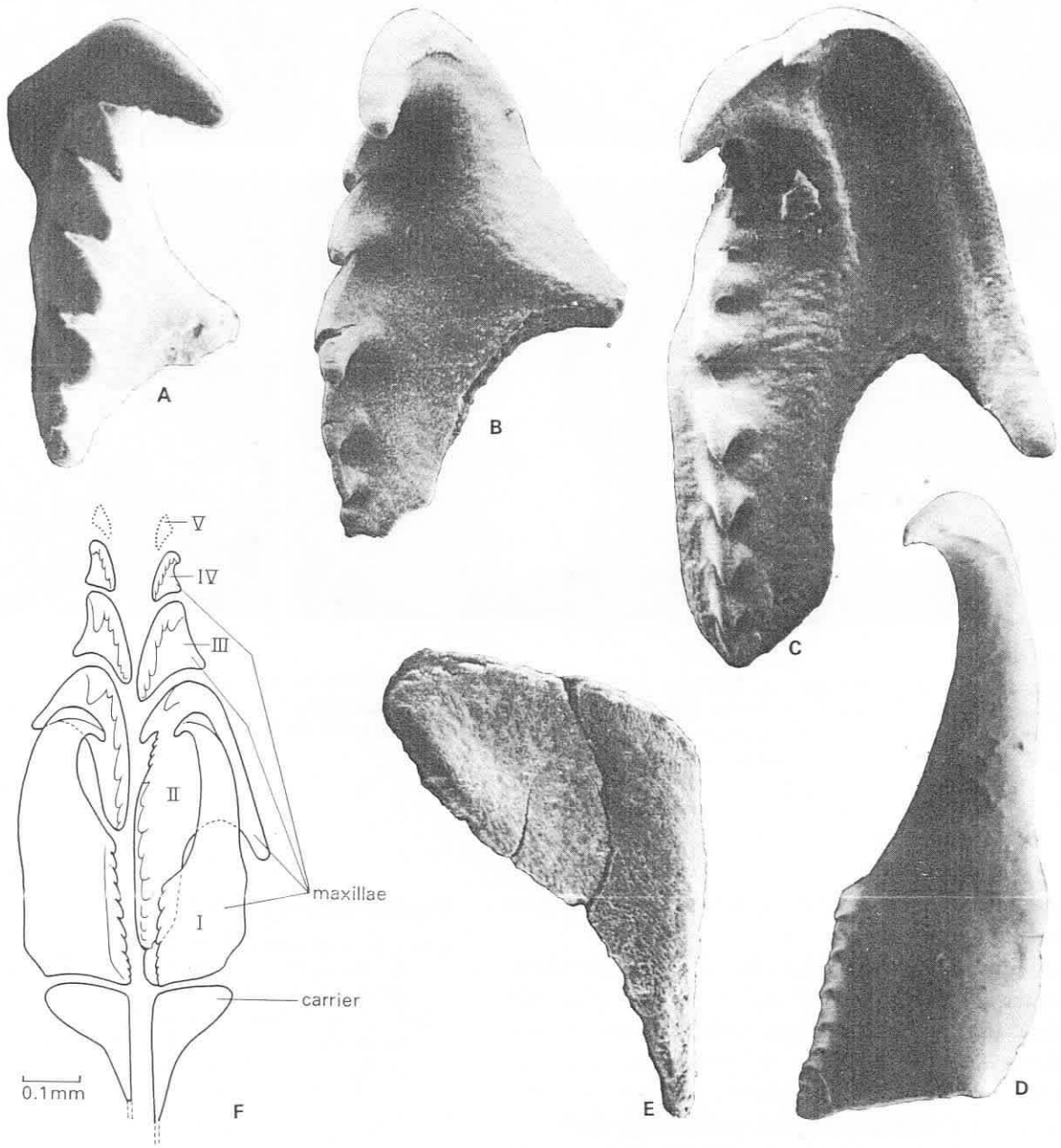


Figure 12.6. Jaw elements (scolecodonts) of the Jurassic polychaete *Arabella* from Poland. A, Right maxilla IV. B, Right maxilla III. C, Right maxilla II. D, Right maxilla I. E, Right carrier in ventral view. F, Reconstruction of jaw apparatus; maxillae V and posterior parts of carriers are unknown. (Modified from Szaniawski, H.; Gaździcki, A. *Acta Palaeontologica Polonica* 1978 v. 23, p. 3–29.)

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